Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head

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The skull of crown birds is profoundly modified from the ancestral dinosaurian condition, featuring an enlarged, toothless premaxillary beak and an intricate kinetic system including a re-engineered palate, reduced temporal arcade, and mobile quadrates. The greatly expanded avian neurocranium protects an enlarged brain and is flanked by reduced jaw adductor muscles. Among fossil taxa recording the transition to the skull of crown birds, the Late Cretaceous toothed bird *Ichthyornis dispar* sits in a pivotal phylogenetic position between stemward early ornithuromorphs and birds of a more crown-like aspect[1-3]. Despite continued work affirming its evolutionary significance[3-8], no substantial new cranial material of *I. dispar* has been described beyond the incomplete and fragmentary remains first recovered in the 1870s. Jurassic and Cretaceous lagerstätten that have yielded important avialan fossils typically preserve crushed and distorted skulls[9]. Moreover, with the exception of *Archaeopteryx*, substantially complete skulls have not been three-dimensionally imaged, severely limiting reconstructions of avialan cranial morphology. Here we report four new specimens of *I. dispar* bearing three-dimensional cranial remains, including a new, extraordinarily complete skull and, unexpectedly, two previously overlooked elements from the well-studied holotype. We used these specimens to generate a near-complete 3D reconstruction of the *I. dispar* skull using high-resolution computed tomography. Our study reveals that *I. dispar* had a transitional beak—small, lacking a palatal shelf, and restricted to the tip of the jaws—coupled with a crown-like kinetic system, demonstrating an earlier origin of the feeding apparatus of crown birds than previously understood and supporting developmentally coordinated transformation of components of this key avian innovation. The brain was relatively modern, but the temporal region was strikingly and unexpectedly deinonychosaur-like, bearing a large adductor chamber bounded dorsally by substantial bony remnants of the upper temporal fenestra. This previously unobserved combination of features

illuminates the transitional states of several diagnostic avian cranial innovations, providing new insight into the assembly of the crown bird skull.

Main Text

The extreme adaptability of the modern bird skull has resulted in spectacular functional disparity across living birds, the largest major terrestrial vertebrate clade[10]. However, the earliest appearances of several modern avian cranial innovations—and their sequence of acquisition—are incompletely known owing to uneven and largely two-dimensional preservation of early ornithuran cranial material[1,3,11,12]. Toward ameliorating this deficiency, we report a newly discovered, nearly complete skull of the iconic early ornithuran *Ichthyornis dispar* housed at the Sternberg Museum of Natural History (FHSM) in Fort Hays, Kansas, USA. One of us (K.S.) discovered the specimen (FHSM VP-18702) in 2014 near Castle Rock in Gove County, Kansas, deriving from the base of MU 10 in the Smoky Hill Member of the Niobrara Formation (Middle Santonian stage, Late Cretaceous).

Using FHSM VP-18702 supplemented by elements from three other undescribed specimens (ALMNH [Alabama Museum of Natural History] 3316, KUVP [University of Kansas Biodiversity Institute] 119673, BHI [Black Hills Institute of Geological Research] 6421) and the holotype YPM 1450, we have assembled a three-dimensional skull reconstruction (**Figure 1**, **Supplementary Information and Plates**) lacking only the vomers, pterygoids, anterior processes of the nasals, stapes, and (presumed) predentary[13]. Referral of all newly described specimens to *I. dispar* is supported by a combination of autapomorphies from across the skeleton (**Supplementary Figure XI**). Surprisingly, we identified two previously unreported cranial elements from the holotype at the Yale Peabody Museum of Natural History (YPM 1450): the first and only known lacrimal from *I. dispar*, and the most complete nasal[3]. Skull material described from *I. dispar* was previously limited to partial

braincases, mandibles, partial quadrates, and small fragments of the maxilla and premaxillary frontal process.

Results and discussion

Given the distorted preservation of most Mesozoic Avialae[9], the reconstructed *I. dispar* skull (**Figure 1**) exceeds in its combination of three-dimensionality and completeness nearly all Mesozoic avialan cranial material other than that of *Archaeopteryx lithographica*[14] and *Hesperornis regalis*[15,16]. In particular, almost uniquely among Mesozoic avialans, the FHSM specimen preserves a complete and relatively undistorted upper temporal and suspensorial region[9]. The reconstructed skull of *I. dispar* illustrates a transitional point in the evolutionary history of the ornithuran skull stemward of Hesperornithiformes, a phylogenetic position recovered by the majority of recent analyses including comprehensive new analyses we have undertaken, bolstered by new characters and character states described here (**Figure 2A**; See **Supplementary Information** and **Supplementary Trees** for our suite of phylogenetic analyses and information concerning the placement of *I. dispar* within Avialae)[11,17].

While the avian stem lineage records numerous transitions towards toothlessness throughout the Mesozoic, the newly observable bill of *I. dispar* records the most stemward three-dimensional information on the origin of the toothless bill of crown birds. Dorsal to the external naris, the upper bill has a concave lateral profile, a derived condition similar to that of many crown birds and Hesperornithiformes but not stemward ornithurans[11] (**Figure 2B, Supplementary Plates VI, VIII, and IX, Supplementary Movies 01 and 05**). The previously undescribed premaxillae are considerably shorter than inferred in previous reconstructions, restricted to the anteriormost quarter of the rostrum. The premaxillae are medially fused, anteriorly pointed, and toothless, unlike those of more stemward ornithurans (*e.g.* the posteriorly unfused, posteriorly toothed premaxillae of *Yanornis martini*). In their

relative length they resemble those of the stemward ornithuromorph *Gansus zheni*[18], which is known from flattened specimens. Because it is more crownward than *Gansus* and relatives, *Ichthyornis* therefore provides polarity to the direction of beak transformation and demonstrates that short premaxillae restricted to the tip of the snout were the plesiomorphic form of the avian beak. In contrast, the more derived toothless tomial margins of the beak in the clade consisting of crown Aves and Hesperornithiformes form the greater part of the lateral margins of the rostral upper jaw[1] (**Figure 2B**). However, *Ichthyornis* shares with this clade, to the exclusion of more stemward ornithurans including *G. zheni*, a decurvature of the premaxilla along the tomial margin. The premaxillae are covered in neurovascular foramina that in living birds often correspond to a highly keratinised region of the rhamphotheca called the premaxillary nail[19]. There is no discernible nasolabial groove running from the naris to the tomial margin; in crown birds, this is an osteological correlate for the rhamphothecal plates posterior to the premaxillary nail[19]. This suggests that the evolutionary origin of the nail preceded the acquisition of other rhamphothecal segments. The ventral surface of the premaxillae[20], observable here for the first time in an ornithuran stemward of Hesperornithiformes, is vaulted dorsally (**Figure 1, 2B**, **Supplementary Plates VI and VIII, Supplementary Movies 01 and 05**), a plesiomorphic dinosaurian condition unlike that of Hesperornithiformes[16] or crown Aves[21] in which a flat palatal shelf is covered by keratinous rhamphotheca (the *palatum corneum*)[22]. The posterior half of the medial tomial margin is dimpled by three conspicuous fossae on each side (**Figure 3B**), which correspond to the occlusal position of the anteriormost dentary teeth. Rostral to these fossae the premaxillae would likely have interacted with a predentary bone, whose presence we infer based on the form of the anterior dentary, the relative length of the lower jaw to the upper, and its presence in other ornithuromorphs[13]. Plesiomorphically and unlike in crown-clade birds, a soft-tissue internarial septum may have been supported by a median ridge extending caudad from the

ventral surface of the premaxillary body onto the ventral surface of the anterior half of the premaxillary frontal process (**Figure 1**, **Supplementary Movie 05**)[20,23,24]. Novel observations about avian evolution from the premaxillae include unambiguous polarization of the short, anteriorly restricted condition as ancestral along the avian stem, the plesiomorphic nature of the palatal surface and extent of the rhamphotheca including early presence of the nail.

The new fossil data from the FHSM and ALMNH specimens enable a reconstruction of the only complete, undistorted ornithuran maxilla known from a taxon stemward of Hesperornithiformes (**Figures 1-2**). Previously only known from a small fragment mistakenly thought to be part of the tooth row (see **Supplement**), the bone was presumed to be considerably shorter than its actual length but is in fact plesiomorphically long. The dentition is extensive in both the upper and lower jaws, occupying nearly the entire length of the dentaries and maxillae, and shows no indication of reduction relative to stemward Avialae; in comparison, the teeth of hesperornithiforms are reduced in size and extent (**Figure 2B**). Distinct sockets are formed by interdental ossifications which develop through ontogeny[25]—a plesiomorphic condition lost in Hesperornithiformes, where the teeth are set in a continuous sulcus[16,26] (and crown Aves, where the teeth are lost entirely). To accommodate dental implantation, the maxillae are robust in lateral view compared to those of crown Aves, in which these bones are reduced to thin, dorsoventrally flattened, predominantly palatal elements[23,24]. However, *I. dispar* shares with more crownward avialans maxillary palatal shelves that are transversely wider than the maxilla is dorsoventrally tall and compose an extensive portion of the bony palate[16] (**Figure 1, Supplementary Movie 01)**. Thus, the maxilla is in some ways plesiomorphic and in others rather crown-bird-like. The ventral surface of each maxillary palatal shelf unexpectedly exhibits a series of occlusal fossae for the lower teeth along the entire caudorostral length of the bone medial to the upper tooth row, a state previously unrecorded in Avialae (**Figure 1, Supplement**). The new material offers

the first clear evidence of the extent of the palatal shelf at an early node within Ornithuromorpha, and the surprising presence of extensive occlusal pits along the length of the palate. The mandibles of *Ichthyornis*, both of which are complete and undistorted in the FHSM skull and at least partly preserved in all of the other new specimens, have already been extensively described based on YPM material (see **Figure 1, Supplementary Plates, and Supplementary Movie 06**)[3,27].

Unexpectedly, we discovered a substantially complete lacrimal — never before described in *Ichthyornis* — and nasal in material composing the *Ichthyornis dispar* holotype YPM 1450, which had remained undescribed and undocumented despite their presence in the YPM collection since 1872[3] (**Figure 1, Supplementary Plate X, Supplementary Movie 04**). The lacrimal is mostly complete, with only the supraorbital and nasofrontal articular region lacking. It is the only known three-dimensional lacrimal from an ornithuran stemward of Hesperornithiformes, and shows that at this stemward node the bone was already similar to that of crown-clade birds[1,9] in being robust, curved caudally, and perforated by a capacious lacrimal foramen. The caudal half of the nasal including the frontal articular region represents a previously unknown portion of the bone anterior to the frontals that helps define the shape of the naris and antorbital fenestra. The frontals, nasals, and premaxillae interdigitated with one another at their articulation on the dorsal surface of the skull such that, like crown Palaeognathae and unlike crown Neognathae, *I. dispar* lacked any indication of a transverse craniofacial hinge between the frontals and nasals[15,21,28,29]. The maxillary process of the nasal remains unknown for *I. dispar*, but the rostral half of the maxilla exhibits a pair of broad articular sulci running along the dorsal surface (**Figure 1, Supplementary Plate VI**): one is located laterally to receive the maxillary process of the premaxillae, and one is positioned medial to the aforementioned sulcus to receive the maxillary process of the nasal. The size of the latter sulcus indicates a broad nasal-maxillary contact and correspondingly broad

postnarial bar[15]. This condition corresponds to that seen in Neognathae, suggesting that the narrow or absent contact and bar of Palaeognathae[21,24,30] is derived within crown birds.

The previously undiscovered palatine, an element rarely preserved in Mesozoic avialans[28], is narrow and elongate (**Figure 1, Supplementary Plate VI, Supplementary Movie 01**), and is similar to that of crown birds: a strong sutural connection to the maxilla as in all known stemward dinosaurs is lost[16]. The next-most-crownward examples of interpretable palatines are from the enantiornithine *Gobipteryx minuta*[28], which has broad, flat palatines with extensive maxillary sutural contact similar to those of *Archaeopteryx lithographica* and non-avialan theropods[14,17]. Thus, the new material reveals that *Ichthyornis* presents the most stemward manifestation of a crown-like avian palatine yet recorded.

The crown-bird-like palatine was linked by the unpreserved pterygoid to a quadrate essentially indistinguishable from that of crown birds (**Figure 1**, **Supplementary Plates V-VII**, **X**, **Supplementary Movie 06**). The FHSM element, unlike all previously described material, is complete and undistorted. Similar to certain Neognathae like Anseriformes, Columbiformes, and the Maastrichtian fossil *Vegavis*, it exhibits two rounded capitular condyles that fit into cotyles on the proötic and squamosal bones to form a mobile joint with the cranium[3,17,21,23]; this raises the possibility that a bicondylar morphology is plesiomorphic for Neornithes. We also identified for the first time the quadratojugal (BHI) and jugals (KU and FHSM) of *Ichthyornis* (**Figure 1, Supplementary Plates V-VI, Supplementary Movie 3)**. The quadratojugal is incomplete, but the articular surface for the quadrate is preserved and would have formed a mobile joint as in crownward taxa. The jugal (FHSM, KU), is deep in lateral view and transversely compressed. The posterior end is forked and would have articulated with the quadratojugal, while the anterior end is pointed and would have laid flat on the dorsal surface of the jugal process of the maxilla. In its depth, the jugal differs from that of most crown birds, where the jugal is more or less rod-shaped. Nevertheless, we can

now conclude for the first time from the tandem arrangement of the rostrum/jugal/quadratojugal bar, the mobile suspensorium, and the narrow, linear palatine, that *I. dispar* possessed a fully functional avian cranial kinetic system, the most stemward known appearance of this key evolutionary innovation[21,23,24].

The virtually complete postorbital cranium of the FHSM skull (**Figure 1, Figure 3, Supplementary Plate VI, Supplementary Movies 2-3**) includes many regions previously undocumented in *I. dispar*, and poorly known in Mesozoic avialans. These include a complete interorbital septum, and postorbital and zygomatic processes. The mesethmoid and parasphenoid rostrum of the FHSM specimen are among the best preserved in any Mesozoic ornithuran[9,15]. The mesethmoid indicates the acquisition of a morphology virtually indistinguishable from that of many crown birds: it is pierced with large fonticuli in the orbital region and does not extend rostral to the frontals, a condition seen in Hesperornithiformes and Neognathae, but not Palaeognathae. With the polarization permitted by the phylogenetic position of *Ichthyornis*, we can now hypothesize that the palaeognath condition, whereby the mesethmoid extends anteriorly to form part of the internarial septum, is autapomorphic[20,24,29].

The endocranial cavity, observable in relatively undistorted sagittal outline for the first time in the FHSM specimen, is essentially crown-like (**Figure 3A**). The forebrain is enlarged and posteroventrally rotated, and the optic lobes are inflated and laterally shifted. Despite mediolateral compression, the overall structure appears more similar to crown birds and the enantiornithine *Cerebavis cenomanica*[31] than to *Archaeopteryx lithographica*[32,33]; to date, these two fossil taxa constitute the only Mesozoic avialans whose endocranial morphology has been characterised.

The FHSM specimen reveals detailed anatomical structure of the temporal and suspensorial region, which is observable for the first time in a Mesozoic avialan stemward of

Hesperornis, The upper temporal fenestra is strikingly expanded (**Figure 1, Figure 3B**), a superficially plesiomorphic feature similar to that of deinonychosaurs and entirely unexpected in an avialan crownward of Enantiornithes. The anterior margin of the fenestra is bounded by a substantial postorbital ossification extending laterally from the skull. This postorbital process resembles the separate postorbital bone of early avialans and non-avialan dinosaurs in extending laterally and then posteriorly (**Figure 3B**), unlike the postorbital process of crown-clade birds, whose apex, even when enlarged (as in multiple modern bird clades including ducks, Anatidae)[24], is directed ventrally[9,15,16,21,34]. Since the postorbital region of the skull is poorly preserved in stemward Avialae, including the three-dimensional yet incomplete cranial remains of *Patagopteryx deferrariisi*[35], it is unclear whether the postorbital ossification in *Ichthyornis* is secondarily enlarged — though, if so, it is enlarged in a way unseen in crown-clade birds and strikingly convergent on non-avialan theropods such as deinonychosaurs (**Figure 3**) — or represents the surprisingly late retention of an ancestral dinosaurian condition. The latter hypothesis would imply the fusion of the postorbital bone to the cranial roof during the course of avialan evolution or its gradual replacement by extensions from the calvarial bones while retaining an ancestral shape. In crown Aves, the postorbital process derives from the combined ossification of the dermal skull roof (as with the ancestral lost or fused postorbital bone), a cartilaginous process on the laterosphenoid, and ossified ligaments and tendons. *I. dispar* shows a crown-bird-like contribution of the laterosphenoid, suggesting that the postorbital ligament and associated temporal musculature exhibited a crown-like configuration as well[20,21,34]. The temporal region is deeply embayed, like that of Hesperornithiformes and non-avialan dinosaurs and unlike that of most extant birds (**Figure 3B**), which generally exhibit reduced adductor chambers, although hypertrophy of the adductor musculature is also seen in some extant aquatic, piscivorous birds such as penguins (Spheniscidae)[16,29,36].

The squamosal — which is preserved in only a handful of Mesozoic avialans such as *Patagopteryx deferrariisi*[35], and among those is heavily damaged or highly derived in all but the relatively crownward and crown-like Hesperornithiformes (see Supplementary Information) — exhibits a plesiomorphic, deinonychosaur-like morphology unseen in crownward taxa including *Hesperornis*: the zygomatic process widely encircles the posterior half of the upper temporal fossa, first projecting laterally and then curving anteriorly such that the process is hooked and directed rostrally (**Figure 3B**). In lateral view, it is deep and triangular. As in non-avialan dinosaurs and unlike in crownward taxa, the nuchal crest along the suture between the parietal and supra- and exoccipitals extends from the midline of the skull onto the squamosal, forming the upper edge of that bone. The majority of the element is plesiomorphically more peripheral to the braincase than in modern birds, where it is highly integrated into the neurocranium[36,37] (**Figure 1**). The morphology of the squamosal in its encirclement of the adductor chamber recalls that of much more stemward, non-ornithuran theropods, such as *Zanabazar junior* (**Figure 3**), where a complete upper temporal arch is still present in retention of the ancestral diapsid condition[17]. Whether or not the enlarged postorbital process is secondary, the nearly complete upper temporal bar may reflect a relatively recent loss of the postorbital and anterior portion of the squamosal or their membranous precursors[38]. Its plesiomorphic appearance suggests that the architecture and topology of the muscles attaching to the posterior part of the upper temporal fossa, which includes the majority of the adductor externus complex[39], likewise exhibited a more plesiomorphic architecture and topology whereas those attaching to the anterior part of the upper temporal fossa, which incorporates the laterosphenoid as in living birds, were more crown-like in their configuration.

In sum, the new and newly identified material represents the most complete, best preserved cranial remains of a Mesozoic ornithuran filling the long phylogenetic gap between

Archaeopteryx and Hesperornithiformes, revealing a stage of avian evolution for which near-complete three-dimensional cranial remains have hitherto been unavailable. Other three-dimensionally preserved skulls populating this portion of the avian stem, such as those of *Patagopteryx deferrariisi* and *Gobipteryx minuta*, are highly incomplete (the former poorly preserved and lacking the rostral portion of the skull, and the latter missing the caudal portion of the skull). Notable novel observations regarding the probable nature of the most recent common ancestor of *Ichthyornis* and crown birds are distributed across the skull. These include the transitional nature of the beak—a cranial module exhibiting especially high evolutionary rates across crown birds[10,40]—permitting us to conclude that the first form of this key avian innovation was that of a plesiomorphically short premaxillary rostrum bearing some transitional features including incomplete rhamphothecal coverage. Also notable are the correspondingly long maxillae exhibiting a plesiomorphically robust structure yet crown-like extensive palatal shelves; the crown-like lacrimal and neognath-like nasal; the essentially modern kinetic apparatus including a crown-like palatine, quadrate, and jugal/quadratojugal bar; the neognath-like ethmoid ossification; and the crown-like endocranial cavity. Certain morphologies revealed by the new specimens are entirely unanticipated, including a temporal region strikingly plesiomorphic in its appearance, characterised by a robust and nearly complete upper temporal bar unlike any in the avian crown. If the enclosure of the temporal region does not represent retained plesiomorphy (strictly, it optimizes as such even assuming *Patagopteryx* is undamaged), this configuration at least represents an example of surprising convergence on non-avialan deinonychosaurian dinosaurs, further emphasizing the conspicuous degree of homoplasy and character reversal that characterizes the Mesozoic phylogenetic history of Avialae[41]. The extensive adductor chamber bounded by a nearly complete upper temporal fenestra coupled with a derived, crown-like brain further challenges a previous suggestion that brain enlargement along the stem of birds drove adductor

reduction owing to spatial restriction during embryonic development[17]. The bill, toothless only in the premaxillary region at its tip, provides the first three-dimensional look at the early stages of this most characteristic and adaptively important of crown avian cranial structures[40]. The pincer-like action of a sharp-tipped, toothless bill would probably have facilitated fine manipulation and preening—essentially performing the role of a surrogate hand as the hands themselves became bound up into wings[17]. Holding and perforation of prey was still likely performed in large part by the large, reptilian tooth row retained and highly developed in *I. dispar*[26]. The concurrent appearance of a crown-grade avian kinetic apparatus would have enabled further precision in grasping as well as expanded gape dimensions. Simultaneous appearance of a modern beak and modern palate is consistent with recently published evidence for a deep molecular developmental linkage between the appearance of the fused premaxillae of the beak and the slimming and detachment of the palatine in the roof of the mouth[42]. Finally, the modernity of the brain of *I. dispar* is consistent with its relatively modern postcranium—locomotion and neural form seem to be tightly linked in birds[33].

Both within the head and between head and body of *I. dispar*, this historically important and phylogenetically pivotal taxon demonstrates the complex and regionalised ways in which evolution acted to form the skull of crown group birds. The data support some previous hypotheses and falsify others in addition to providing some entirely unexpected insights. These new observations help fill a gap in our knowledge of avian cranial evolution spanning over 60 million years and virtually the entirety of avialan phylogenetic history.

Methods

Ichthyornis dispar specimens housed at ALMNH, BHI, FHSM, KUVP, and YPM, were scanned at the University of Texas High-Resolution CT Facility (UTCT), and the Center for

Nanoscale Systems at Harvard (CNS). Scan parameters and specimen details are presented in the **Supplementary Information**.

Scanned cranial material was digitally segmented using VGStudio MAX 3.0, and 3D surface meshes were extracted and imported to MeshLab 2016 for optimisation. Optimised meshes were then assembled into 3D reconstructions using Autodesk Maya 2017.

Supplementary Information

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions

D.J.F. and B.-A.S.B. conceived and directed the study and arranged logistics of specimen preparation and CT scanning. K.S. discovered the FHSM specimen and donated it to the museum. D.J.F., M.H., and B.-A.S.B. performed CT scans and processed CT data. M.H., D.J.F., and B.-A.S.B. scored characters and performed phylogenetic analyses. B.-A.S.B. and M.H. planned the main text figures and M.H. assembled the skull reconstruction. M.H. and D.J.F. prepared figures. D.J.F. wrote the supplementary anatomical descriptions and rendered the supplementary videos. D.B., L.E.W., K.S., D.E., and J.E. collected and prepared specimens for study, analysed morphology, and edited the paper. B.-A.S.B., D.J.F., and M.H. wrote the paper. D.J.F. and B.-A.S.B. acquired funding.

Author Information

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Figures

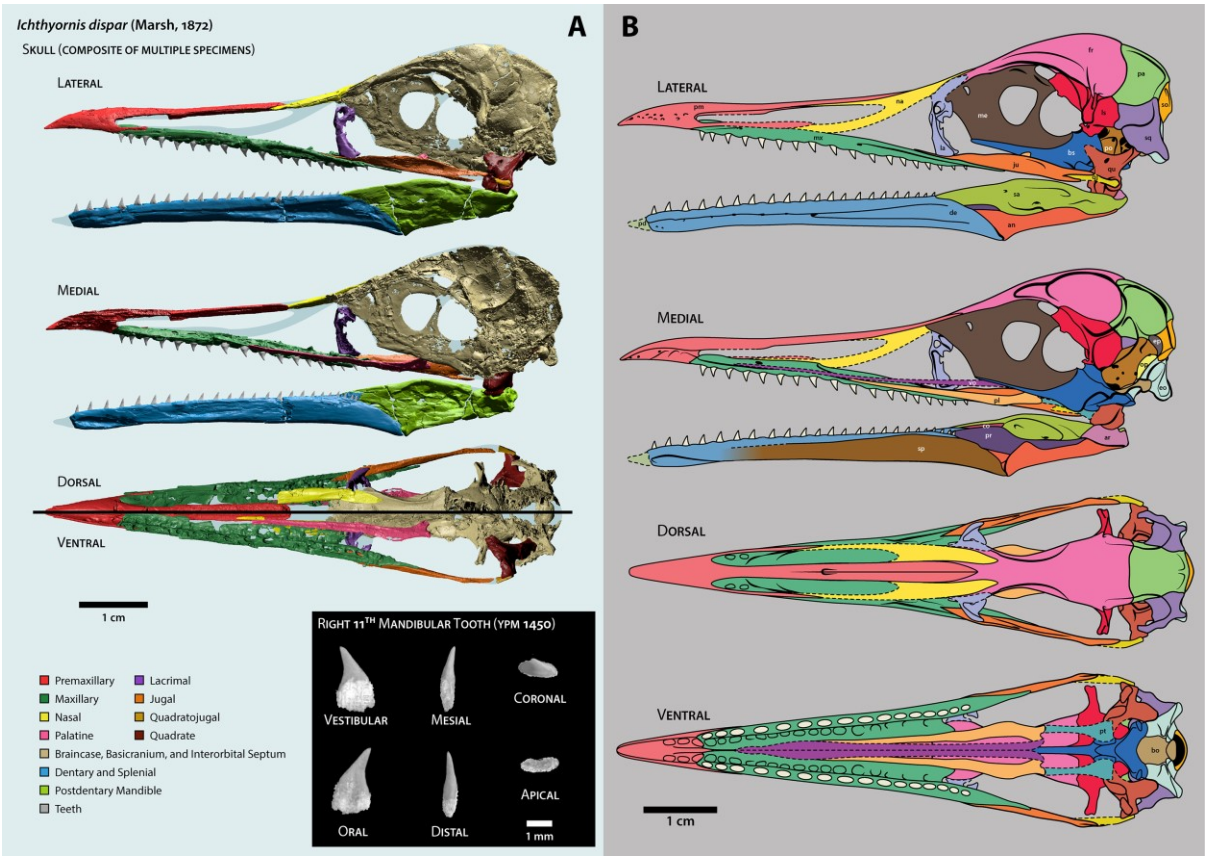


***Figure 1. A**:* Full 3D reconstruction of the skull of *Ichthyornis dispar*. Details in **Supplementary Information**.

***B**:* Line drawing of the skull of *I. dispar*, solid lines indicate areas known from fossil specimens, dashed lines indicate unknown areas reconstructed from other ornithuran birds. Anatomical Abbreviations. an: angular; ar: articular; bo: basioccipital; bs: basisphenoid; co: coronoid; de: dentary; eo: exoccipital; ep: epiotic; ju: jugal; la: lacrimal; ls: laterosphenoid; fr: frontal; me: mesethmoid; mx: maxilla; na: nasal; op: opisthotic; pa: parietal; pl: palatine; pm: premaxillae; po: proötic; pt: pterygoid; qj: quadratojugal; qu: quadrate; sa: supraangular; sp: splenial; sq: squamosal; vo: vomer.

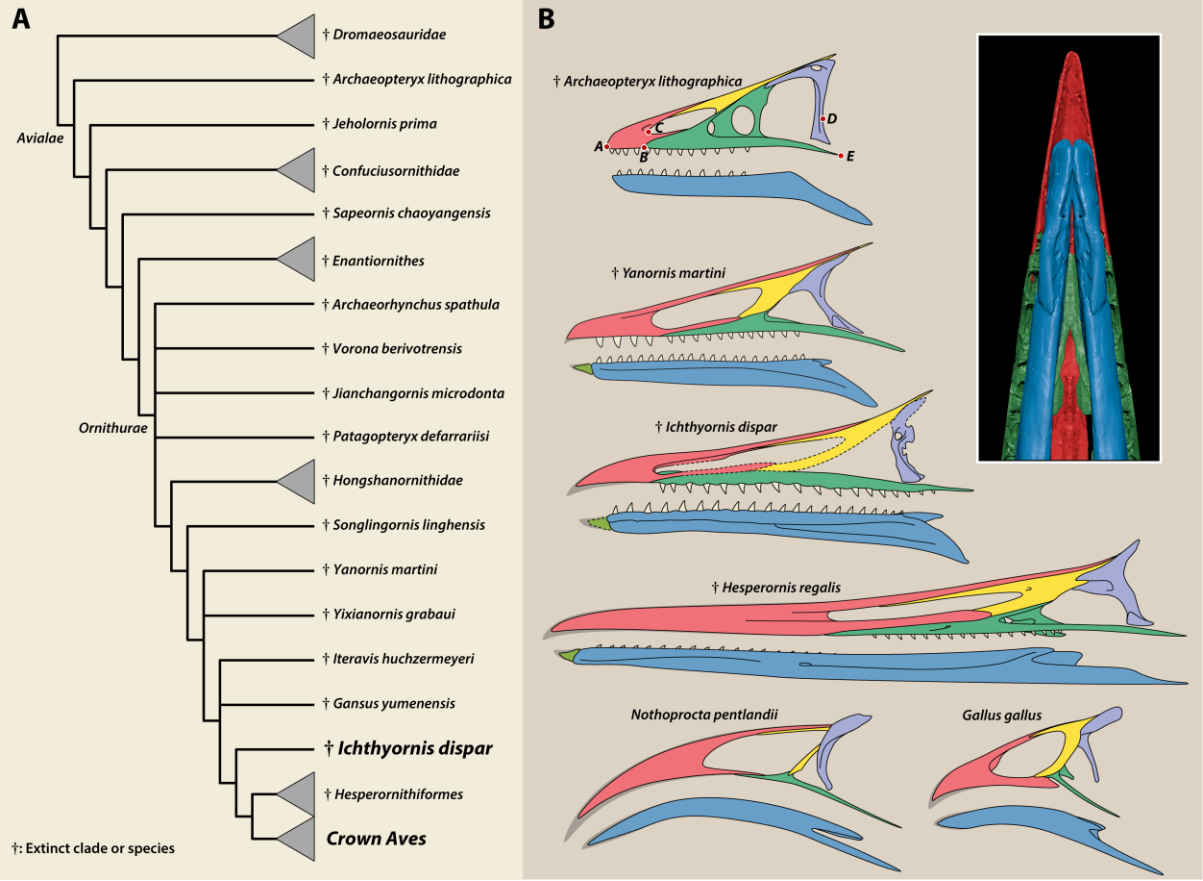
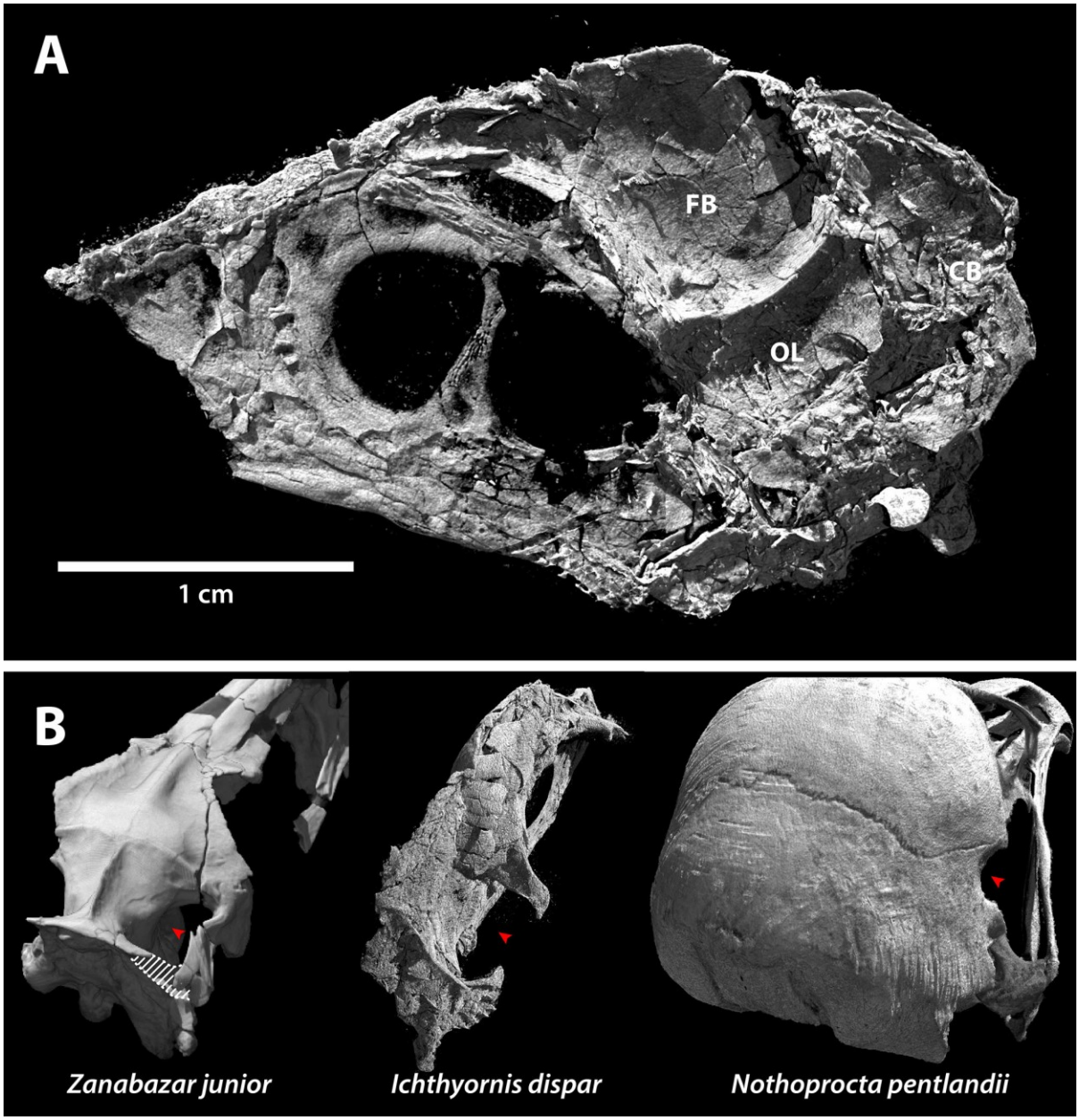


Figure 2. A: Cladogram showing the phylogenetic position of *Ichthyornis dispar* inferred based on novel analyses (abridged and based in part on new codings in multiple datasets; see **Supplementary Information** for full phylogenetic results).

B*:* Origin of the avian bill. Line drawings of the rostrum of key Mesozoic avialans and crown birds (see **Figure 2A** for phylogenetic position). Hypothesised extent of rhamphotheca is indicated in grey. Points on the rostrum of *A. lithographica* denote landmarks used for comparative measurements presented in the **Supplementary Information**. Inset shows the occlusal gap between the tips of the premaxillae (red) and dentaries (blue) in ventral view that may have been occupied by a predentary.



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381 ***Figure 3. A***: Sagittal cutaway of the braincase of *Ichthyornis dispar* revealing the endocranial
382 space. Cavities labelled for brain divisions as follows — FB: Forebrain, OL: Optic lobe, CB:
383 Cerebellum.
384 ***B****:* Comparative views of the temporal region of a nonavian dinosaur (*Zanabazar junior*),
385 *Ichthyornis dispar*, and a crown bird (Andean Tinamou, *Nothoprocta pentlandii*). Red arrows
386 denote position of the upper temporal fenestra.

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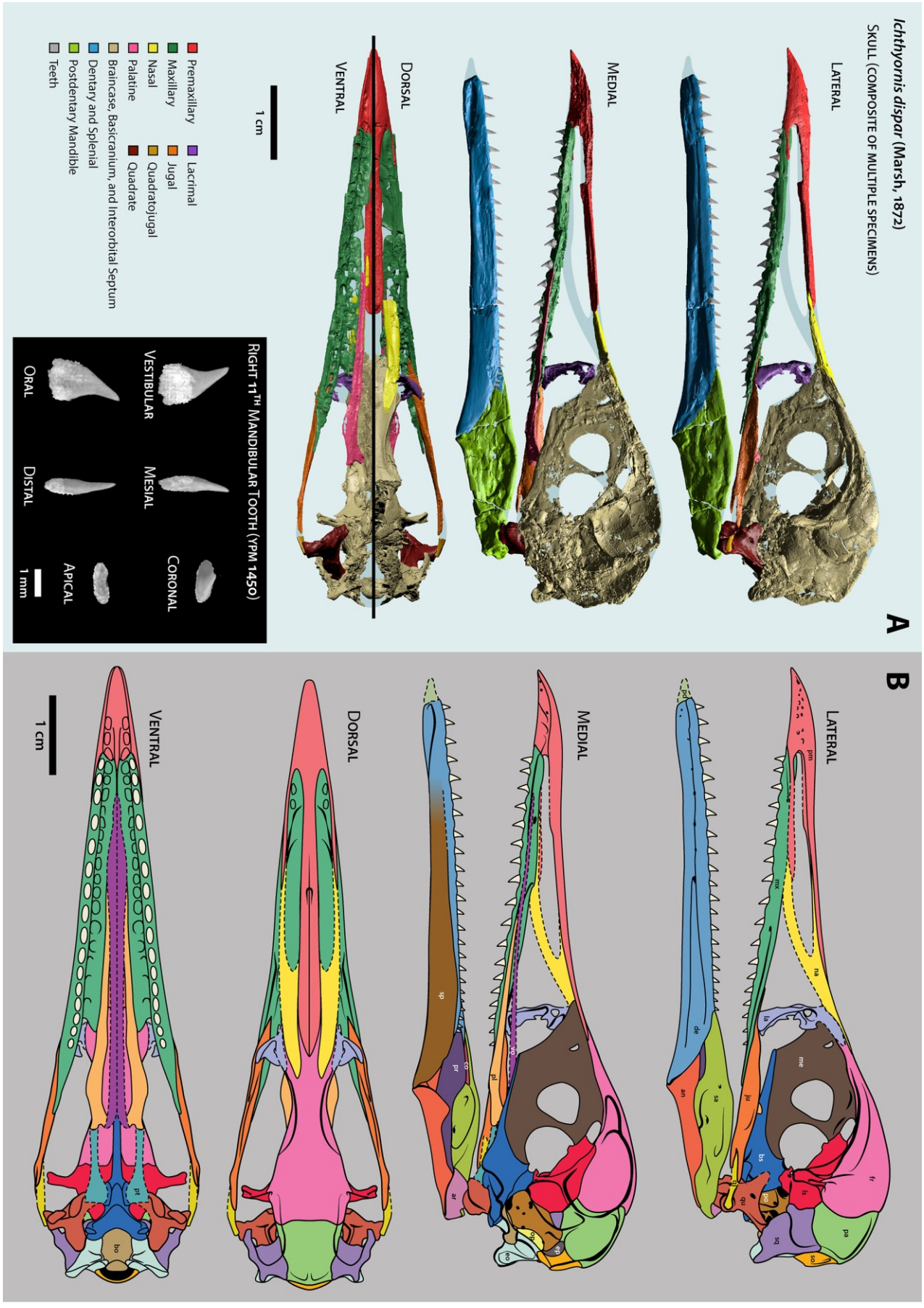

388 ***Figure 1 enlarged***

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